THE *MARTINIOPSIS*-LIKE SPIRIFERIDS OF THE QUEENSLAND PERMIAN

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ABSTRACT. The three brachiopod genera *Martiniopsis* Waagen, *Notospirifer* Harrington, and *Ingelarella* nov. are included in the new subfamily Ingelarellinae of the family Spiriferidae. The detailed morphology of the group is discussed, *Notospirifer* is redefined, and *Ingelarella* and its type species are described. It is concluded that *Martiniopsis* is restricted to the Tethyan–Ural area, while *Notospirifer* is as yet recorded only from Australia, and *Ingelarella* occurs in Australasia, Argentina, and possibly Pakistan and Kashmir. All three genera appear to be restricted to the Permian (Sakmarian–Tartarian).

INTRODUCTION

SINCE the work of Etheridge (1892) no critical work has been done on the spiriferid brachiopods from the Queensland Permian which are commonly placed in *Martiniopsis* Waagen. It has been customary to refer all specimens to *M. subradiata* (Sowerby) and its sub-species, *M. darwini* (Morris) or *M. oviformis* (M'Coy). Representatives of the group are found throughout the marine Permian deposits of the State, often in great abundance, and they exhibit a very wide range of variation. There are two genera involved—*Notospirifer* Harrington and *Ingelarella* nov.—which together are represented by some twenty-three species. The species all have a fairly restricted stratigraphic range, and it has been found possible to use them for correlation on both a regional and inter-basinal scale. No forms referable to *Martiniopsis* Waagen have yet been discovered, and it now appears that that genus was restricted to the warmer waters of the Tethyan–Ural region, while *Notospirifer* and *Ingelarella* characterize the cooler water Gondwana province.

Family SPIRIFERIDAE King 1846

Subfamily INGELARELLINAE nov.

Diagnosis. Spiriferidae of very variable size; hinge line variable in length but always less than the maximum width of the shell; cardinal extremities rounded; fold and sinus present or absent; commissure rectimarginate to parasulcate and sulciplicate; cardinal areas invariably present on each valve; delthyrium partly obstructed by narrow dental ridges; lateral slopes smooth or bearing up to six deep rounded plications; shell substance in two layers—a very thin 'epidermoidal' layer and a thick inner fibrous layer; outer layer bearing shallow pits of variable shape; teeth supported on well-developed dental lamellae; ventral adminicula diverge at variable angles; dorsal adminicula range in length from one-third the length of the valve to absent; crural plates strong; spires with from about twelve to twenty-five volutions; no jugum present.

Remarks. This subfamily is erected to include *Martiniopsis* Waagen, *Notospirifer* Harrington and *Ingelarella* gen. nov. I have erected it on *Ingelarella* gen. nov. in preference to *Martiniopsis* Waagen or *Notospirifer* Harrington, because the former genus is much more adequately known, and because of the inaccessibility of type material of *Martiniopsis*,

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and my inability to locate the type locality of *Notospirifer darwini* (Morris), the type species of *Notospirifer*. In his original work Waagen placed the genus *Martiniopsis* in the subfamily Martiniinae (Waagen 1883), and most subsequent authors have acquiesced in this assignment (Schuchert and Le Vene 1929; Douglas 1940). Tschernyschew, however, put it in the Delthyrinae. The apparent similarity of *Martinia* and *Martiniopsis* is, however, due to homeomorphy and there is little similarity between *Martinia* and the other genera here included in the Ingelarellinae. Fredericks (1926), basing his subfamilies primarily upon the internal structure of the pedicle valve, separated *Martiniopsis* from *Martinia* and placed it in the section 'glabratae-levis' of his subfamily Munellinae in which apical plates are developed. The artificiality of this classification has been pointed out by several authors (George 1933; Maxwell 1954), and most workers find it quite unacceptable except as a classificatory key.

In the opinion of Harrington (1955), *Notospirifer* is a member of the Phricodothyrinae Caster, but this assignment is the result of a misconception of the nature of the ornament of his genus. As is shown hereunder, *Notospirifer* bears a superficial ornament of surface pits, and not spines as do the phricodothyrinids; and further, it does not have the reticulate shell structure of that group.

Australian authors dealing with the so-called *Martiniopsis* of eastern Australia have never classified them under a subfamily.

SHELL STRUCTURE

Of the shell structure of *Martiniopsis*, Waagen (1883, p. 524) reported: 'The shell is coated with an epidermis which exhibits a very distinct punctation, very similar to the punctation of *Terebratula*. The median shell layers show this punctation much less distinctly, though it can be well observed in places. The punctation is very fine, close, and arranged in quincunx.' Opposed to this is the conclusion of Browne (1953, p. 103) that the Salt Range specimens which she examined were impunctate, and that the so-called punctation is no more than a delicate surface ornament.

Morris (1845, p. 281) was the first to remark on the punctation of Australian specimens, and he apparently appreciated the fact that it was a superficial phenomenon—'the surface of the shell marked by numerous, minute, elongated punctations . . .'. de Koninck (1877, p. 178 English translation) considered that the surface of forms referred by him to *Spirifer darwini* was covered with granulations rather than punctations, but this was apparently the result of faulty observation. The same author relegated certain Ingelarellinids to *Spirifer glaber*, but noted that the test was thin and perforated, and that 'the whole surface is covered with well marked punctures arranged quincuncially'.

Etheridge observed the shell structure of Ingelarellinids from numerous localities in eastern Australia, presenting his conclusions in two works (1892, pp. 238–9; 1919, p. 185), but it would appear that he was never certain of the intimate structural details. Of some Queensland specimens he states: 'Wherever the surface is abraded this striation has the appearance of longitudinal tubes running through the substance of the test; but on those portions merely smoothed over by the denuding agent, these tubes appear as darker lines traversing the lighter coloured limestone of which the shell is composed' (1892, p. 239). It is difficult to conclude from this whether he believed the 'tubes' in question to be punctae or not. After an examination of specimens from the New South Wales South Coast he reported that: 'It would appear as if some layers of the test were

fibrous, others punctate, hence I used the term "punctate-fibrous"' (1919, p. 185). However, in well-preserved specimens from the Upper Marine of the Hunter Valley 'there is visible on the exteriors a remarkably delicate and fine, longitudinal, tear-like sculpture, which may be of an epidermal nature, but it is not accompanied by perforations, so far as I can see'.

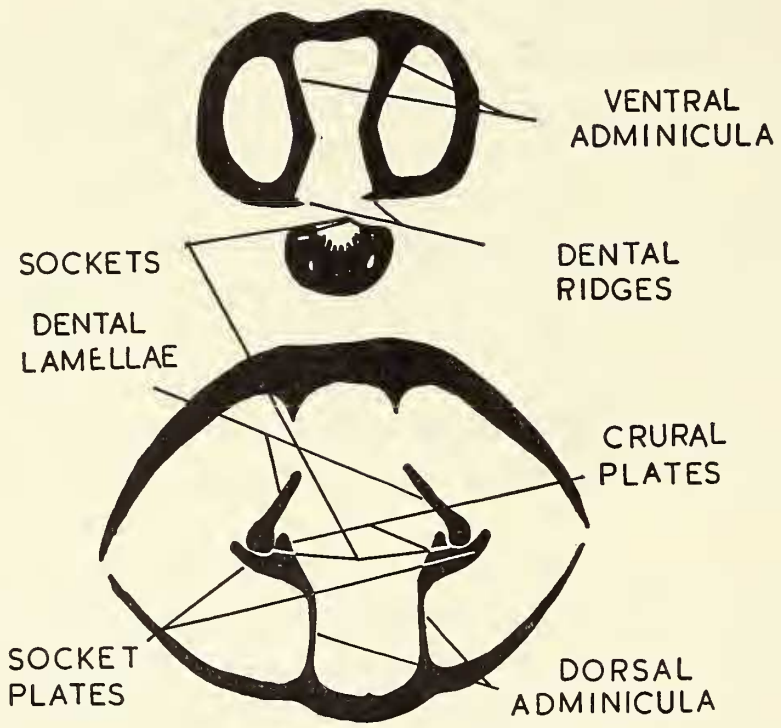
In this study I have examined thin sections of the shells of several species of both *Ingelarella* and *Notospirifer* and have reached the following conclusions: (1) In both *Ingelarella* and *Notospirifer* the wall is composed of two distinct layers, a thin outer layer and a thick inner fibrous lamellar layer, often referred to as the primary and secondary layers (cf. Williams 1956). (2) The outer layer is much thicker in *Notospirifer* than *Ingelarella*. This layer (the epidermis of Waagen and Etheridge) carries quincuncially arranged pits, and this therefore accounts for the difference in the depth of the pits in the above genera. It covers the whole outer surface of the valves. The fibres of which it is composed are very fine (usually visible only at magnifications above 50), and are arranged with their length approximately at right angles to the surface of the shell. (3) The inner layer is formed of layers of fibres which in longitudinal section are inclined obliquely forward from the outside to the inside of the shell. Within each layer the fibres are subparallel, but they are highly irregular in direction. At any position in the shell the fibres within neighbouring layers run in different directions. (4) No endopunctae are present.

In a thin section of an undescribed species of *Ingelarella* from Homevale, several small spicular structures composed of structureless calcium carbonate have been observed to run obliquely across the lamellae. The fibres in which they are embedded are arched around them. They are few in number and are irregularly distributed, and certainly are not of sufficient size or abundance to warrant comparison with the pseudo-punctate type of shell structure found in such groups as the stropheodontids. Thin sections of other species have failed to reveal further examples, but specimens of another species from near Theodore show fairly numerous irregular pits in decorticated specimens, which may indicate the presence of spicules. Unfortunately several attempts to prepare thin sections of this material have proved unsuccessful. Specimens of the type species from Mt. Coma (see Pl. 57, fig. 5*a*) show evidence of the projecting ends of these spicular structures in internal moulds.

Surface pits. Surface depressions, which vary in shape from circular pits to linear furrows, and which are restricted to the outer (prismatic) layer of the shell, are found in all members of the subfamily. These structures fall within the definition of Schuchert and Cooper's *exopunctae*. Williams (1956, p. 250) has pointed out that this term has been used to cover several structures of different origin, and hence it has not been used in this work.

In *Ingelarella* the surface pits are elongate, narrow and shallow, and would perhaps be better described as delicate furrows. They are usually broadest and deepest in their median portions, and taper toward each end. In some species, however, some pits are broadest and deepest toward the umbo and taper abruptly posteriorly and gradually anteriorly. Pits commonly transgress the growth laminae. Their size may vary from lamina to lamina, particularly on the anterior part of the shell, probably indicating periods of seasonal growth. There is little doubt, however, that in general the shape, size, and arrangement of the pits are of specific value.

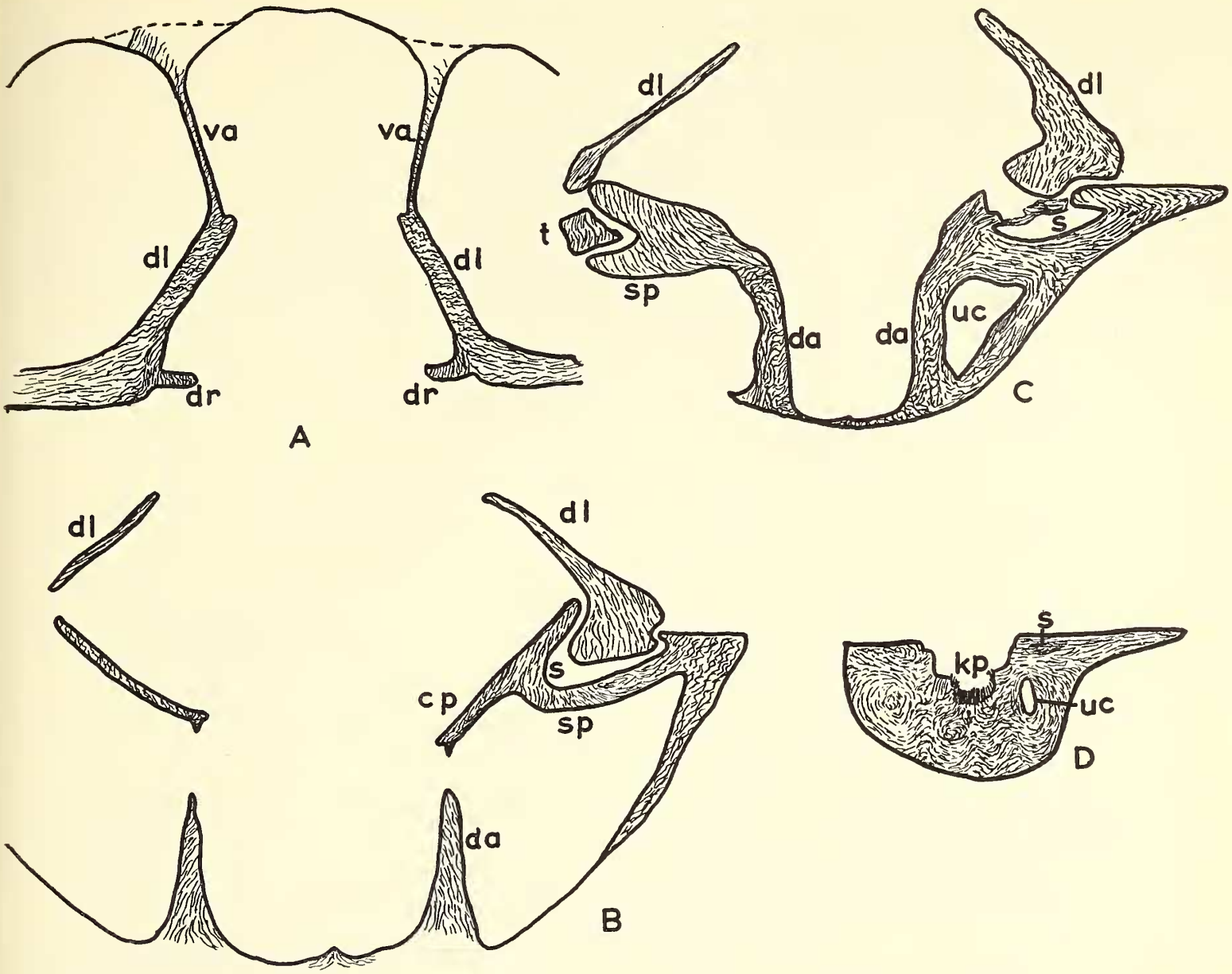
The pits of *Notospirifer* are deeper, coarser, and more closely packed than in any species of *Ingelarella* with which I am acquainted. In addition their outline is also more nearly equidimensional, in some cases being almost circular. The size and shape of the pits varies in some specimens in an irregular manner, e.g. a specimen from Homevale shows sub-circular pits on some portions, oval on others, and diamond shaped on yet others (cf. Etheridge 1919, pl. 28, fig. 2). Other specimens show a weak seasonal variation in size of the pits on the adult stages.



TEXT-FIG. 1. Two diagrammatic sections across the umbonal region of *Ingelarella* illustrating the terminology applied to the internal structures of the Ingelarellinae.

Internal structures. In the apex of the pedicle valve is a central thickening which is continued forward as a very short septum dividing the posterior end of the muscle field. This thickening is continuous with the outer wall of the shell and is composed of irregularly arranged fibres. Contiguous with it apically, but diverging forwards, is a pair of plates, formed as an ingrowth of the outer wall, and composed of curved fibres which sweep forwards and inwards. They are thickest near the umbo and thin out rapidly forwards, where they form a lining to the posterior third of the delthyrial cavity. Their function is not apparent, and they may be merely 'connective' tissue filling in the umbonal area, and hence they are herein referred to as pleromal plates ($\pi\lambda\eta\rho\acute{o}\omega$ = I fill). The adminicula (Browne 1953, p. 102) lie between the pleromal plates and the outer shell wall and are formed of tissue continuous with the inner-wall layer. The fibres of which they are formed are arranged roughly at right angles to their surface, though there are many irregularities.

At an early stage in ontogeny a thin layer begins to become differentiated on the inner side of the adminicula just inside the delthyrium and along the edge of the cardinal area. From the outset these differentiated portions, which develop into the dental lamellae, carry short processes which line the edge of the delthyrium and extend anteriorly into the teeth. These are referred to as dental ridges. The dental lamellae increase in height and thickness toward the front. Their structure is fibrous. the fibres being arranged



TEXT-FIG. 2. Sections through specimens of *Ingelarella angulata* sp. nov. showing the fibre arrangement in various plates. A, section of the pedicle valve just behind the hinge line; B, slightly oblique section taken through one tooth and anterior to the other; C, slightly oblique section taken posterior to one tooth and through the other; D, section through a brachial valve showing the cardinal process and the very apex of the right dental socket. cp, crural plate; da, dorsal adminiculum; dl, dental lamella; dr, dental ridge; kp, cardinal process; s, socket; sp, socket plate; t, tooth; uc, umbonal cavity; va, ventral adminiculum.

parallel with their length, and their outer surfaces are lined by the adminicula for a greater or lesser distance depending on the species.

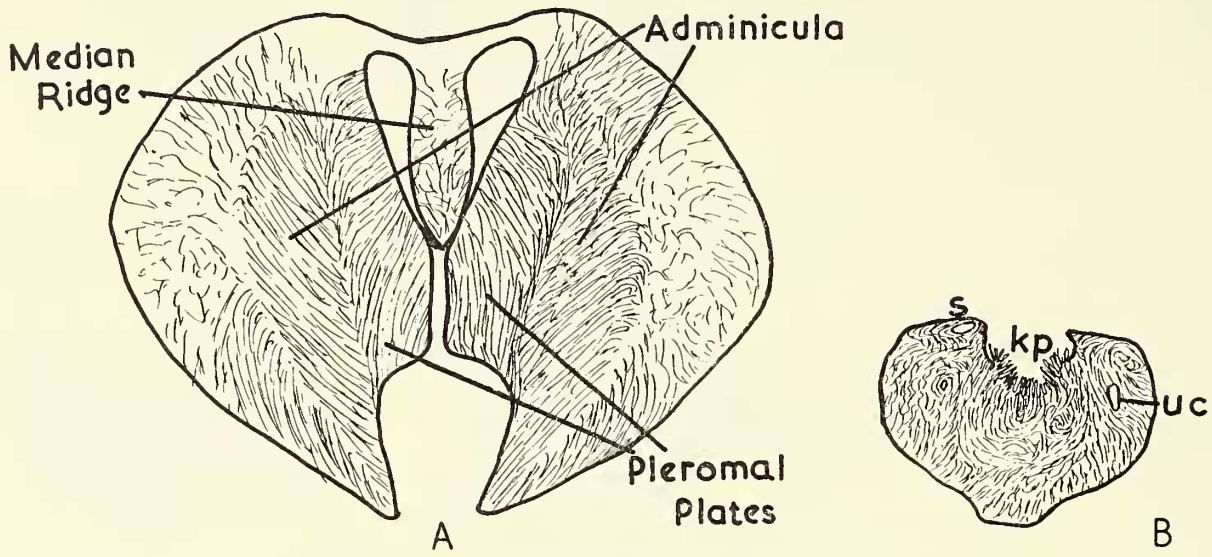
The apex of the notothyrial cavity of the brachial valve is lined with a thick fibrous layer, from the inner surface of which the plates of the cardinal process are developed. This layer becomes progressively thinner anteriorly and does not appear to reach the posterior limits of the muscle scars.

The apex of the dental sockets is carried in a distinct fibrous layer lining the cardinal area. This layer is welded on to the outer wall of the shell and the infolded dorsal adminicula. As the sockets develop, a very thin covering plate is retained over their ventral (outer) surface, but the remainder of the socket layer becomes thickened, and a projection from their inner edges forms a carina along the ventral edge of the notothyrial cavity in most species. It is from this carinate portion that the descending lamellae of

the spires subsequently develop. Anteriorly, the adminicula, which serve as supports for the socket complexes, decrease in height and the latter become free. The median carina is formed by a slight thickening of the shell.

Genus MARTINIOPSIS Waagen 1883

Type species by subsequent selection of Etheridge (1892, p. 238): *Martiniopsis inflata* Waagen 1883. As Browne (1953) has pointed out, Etheridge made the first formal designation of the type species, though this has been overlooked in favour of the designation of Hall and Clarke (1894).



TEXT-FIG. 3. Sections through specimens of a large undescribed species of *Ingelarella* from the Homevale district showing the fibre arrangement in various plates. A, section through the pedicle umbo showing the median and pleromal plates and the adminicula; B, section of a brachial valve through the lower part of the sockets. Symbols as for text-fig. 2.

Diagnosis. Small Ingelarellinids with length approximately equal to width; hinge line very short and cardinal extremities well rounded; sinus and fold not developed; commissure rectimarginate to sinuate; lateral slopes non-plicate, smooth; surface ornamented with quincuncially arranged pits of unknown shape; ventral adminicula and dental lamellae well developed; dorsal adminicula long and thin.

Remarks. Waagen (1883) placed two species *M. inflata* and *M. subpentagonalis* in his genus *Martiniopsis*, the former being recorded only from the Upper *Productus* Limestone of the Salt Range, while the latter 'seems to be a species characteristic of the lower division of the *Productus* Limestone'. *M. subpentagonalis* was considered to be distinguished by its 'much flatter valves, a more prominent beak and a more distinct cardinal area than *M. inflata* . . .'. Although both dental and crural plates were described by Waagen the details of the internal structure of the genus have remained unknown until recently, when Dr. Ida Browne (1953, p. 103) published serial sections of a specimen from the Lower *Productus* Limestone at Amb. On the basis of a graphical analysis of external characters, an attempt was made to show that *M. subpentagonalis* and *M. inflata* are conspecific, and hence that the figured serial sections, which are from a specimen from the type locality of *M. subpentagonalis*, are in fact typical of the type species. With the information available at present it is, in my opinion, impossible to prove conclusively that these two species are conspecific. However, the work of Waagen (1883) and Browne

(1953) shows that they are similar in external form, ornamentation, and in the presence of ventral and dorsal adminicula, so that there is little doubt that they are congeneric. Though attempts have been made to obtain topotypes of *M. inflata* these have not met with success, and hence I am here interpreting the internal structure of *Martiniopsis* on the sections figured by Browne (1953, p. 101). It is to be noted that no details are yet available on the muscle scars of either valve of the Indian species.

Distribution. In general it has proved difficult to assess the accuracy of many references to *Martiniopsis* because of inadequate illustrations and the lack of descriptive detail concerning internal characters and surface ornament.

Permian species placed in Martiniopsis

Name and reference	*Locality and stratigraphical position*	*Age*
M. inflata Waagen in Waagen (1883)	Upper *Productus* Limestones of Salt Range	Tartarian
M. subpentagonalis Waagen in Waagen (1883)	Lower *Productus* Limestones of Salt Range	Artinskian
M. latouchei Diener in Diener (1911)	'*Fusulina*' Limestone of Kehsi Mansam, Shan States	Tartarian
M. cathaysiensis Grabau in Grabau (1936)	Maping Limestone of Kweichow and Kwangsi	Sakmarian
M. uralica Tscher. *M. orientalis* Tscher. in Tschernyschew (1902)	'*Schwagerina*' Limestone of the Urals	Sakmarian and Artinskian

Doubtfully placed in Martiniopsis

M. uralica Tscher. and *M. orientalis* Tscher. in Mansuy (1913)	*Productus* Limestones of Laos and Tonkin	? Artinskian
M. inflata Waagen in Mansuy (1912)	Yunnan	? Artinskian
M. inflata Waagen. *M. convexa* Tscher. *M. orientalis* Tscher. *M.* cf. *lutugini* Tscher. in Grabau (1934)	Chihsia Limestone of Kweichow	Artinskian
M. subaviformis Grabau in Grabau (1936)	Maping Limestone of Kwangsi	Lower Sakmarian
M. lutugini Tscher. *M. convexa* Tscher. in Tschernyschew (1902)	'*Schwagerina*' Limestone of the Urals	Sakmarian and Artinskian
M. uralica Tscher. *M.* n. sp. ind. aff. *convexa* Tscher. *M. laticollis* Merla in Merla (1934)	Karakorum	Lower Permian
Spirifer (*Martiniopsis*) *talishaoensis* Reed in Reed (1927)	Yunnan	? Artinskian

Not placed in Martiniopsis

M. baschkirica Tscher. *M. b.* mut. *indosiniensis* Mansuy in Mansuy (1913)	*Productus* Limestones of Laos and Tonkin	Artinskian
M. ? *bashkirica* Tscher. *M.* ? *orientalis* Tscher. in Ozaki (1931)	North China	Permian
Martinia nucula Broili, see Branson (1948, p. 418)	Timor	Permian
M. baschkirica Tscher. in Hayasaka (1922)	Manchuria	Permian

M. aschensis Tscher. *M. bashkirica* Tscher. in Tschernyschew (1902)	'*Schwagerina*' Limestone of the Urals	Sakmarian and Artinskian
Spirifer interplicatus Rothpletz var. *bashkirica* Tscher. in Heritsch (1935): see Branson (1948, p. 417)	Lower *Schwagerina* Limestone of the Carnic Alps	Sakmarian
Martiniopsis sp. in McLearn and Kindle (1950, p. 33)	Mt. Merrill, British Columbia	? Permian

The above determinations are made on the basis of the available literature only, except in the case of the last-mentioned form. In this instance the specimens concerned were made available by Dr. Peter Harker of the Canadian Geological Survey. I consider them to belong to the Rostrospiracea.

Occasional specimens from outside the Permian have been referred to the genus. A lower Carboniferous form from Novaya Zemlya was considered to be a *Martiniopsis* by Lee (1909, p. 159), but its multi-plicate lateral slopes, plicate sinus, and the linear arrangement of its micro-ornament, clearly show that its affinities are elsewhere. From the mid-Devonian of Ohio and Nevada and the Upper Devonian of New York come three species which Cooper (1944, p. 329) has tentatively referred to '*Martiniopsis*'. Dr. Cooper has kindly provided me with specimens of '*M.*' *laevis* Hall from the Ithaca Formation of New York. One well-preserved exterior shows a regular and closely set, fine, concentric ornament, crossed by close, very delicate striae. The interior of the brachial valve shows two short plates (no more than 1 mm. in length) immediately beneath the umbo, but it is not clear from the specimens available whether these are adminicula or the result of the direct union of the crural plates with the shell wall. Hall's figures (1867, pl. 39, figs. 3, 5, 6) show a well-developed pseudodeltidium, and fig. 7 shows a marked plication of the anterior portions of the lateral slopes unknown in *Martiniopsis*. In contour and outline this species resembles some species of *Ingelarella*, but there is no doubt that the resemblance is due to homeomorphy.

Martiniopsis thus appears to be restricted in time to the Permian (or possibly to the Uralian and Permian), and in space to the Asian Tethys and its offshoots in the Ural and Cathaysian troughs. In all areas it appears to be associated with warm-water limestone deposits which contain fusulines. It is significant that the genus has not been recorded in the pre-*Productus* Limestone formations of the Salt Range (Sakmarian) which are of a cold-water facies, though it occurs in the Sakmarian limestones of the Urals; and further, no genuine record of it has come from the other cold-water areas of Gondwana.

INGELARELLA gen. nov.

1845 *Spirifer* Sowerby; Morris (in part), p. 281, pl. 15, figs. 5, 5*a*; pl. 16, figs. 1, 4.
1872 *Spirifera* Sowerby; Etheridge (in part), p. 330, pl. 16, figs. 3–5.
1877 *Spirifer* Sowerby; de Koninck (in part), p. 177, pl. 11, fig. 8, pl. 12, fig. 1; p. 179, pl. 10, fig. 11, pl. 11, fig. 10, pl. 16, fig. 1; p. 181, pl. 12, fig. 3; p. 183, pl. 13, fig. 1, pl. 14, fig. 1 (page and plate numbers refer to the English translation of 1898).
?1891 *Martiniopsis* Waagen; Waagen, pp. 131–2, pl. 5, figs. 9*a*, *b*, *c*.
1892 *Martiniopsis* Waagen; Etheridge, pp. 236–41, pl. 11, fig. 14; pl. 9, figs. 13–14; pl. 39, figs. 5–7; pl. 11, figs. 12–13.
1892 *Spirifera* Sowerby; Etheridge (in part), p. 234, pl. 10, figs. 5–7.
1919 *Martiniopsis* Waagen; Etheridge, pp. 184–6, pl. 28, figs. 1, 5–6; pl. 29, figs. 1–2.
?1932 *Spirifer* (*Brachythyris*) M'Coy; Reed, pp. 27–28, pl. 5, figs. 10–12.
1955 *Notospirifer* Harrington; Harrington (in part), pp. 115–17, pl. 23, figs. 3–6, 8–10, 13, 15.

Type species Ingelarella angulata sp. nov., from the Ingelara Shale, Queensland.

Diagnosis. Shells small to large in size; fold and sinus present, but very variably developed, and each with or without a median furrow; lateral slopes smooth or exhibiting varying degrees of plication; pedicle umbo usually high; hinge about two-thirds the maximum width of the valve; shell formed of two layers, the outer usually being of the order of $\frac{1}{25}$ mm. thick, and carrying a series of fine semi-quincuncially disposed short linear depressions; dental lamellae and ventral adminicula present, the latter never lying completely lateral to the folds bordering the sinus; sockets long; crural plates and dorsal adminicula always developed; descending lamellae robust, and spires directed posterolaterally.

Remarks. *Martiniopsis* Waagen differs from this genus in its lack of a median fold and sinus, its smaller size and the absence of plication on the lateral slopes.

Within the genus three stocks have been recognized, each of which may possibly be worthy of sub-generic rank.

(*a*) The type stock of *I. angulata* which includes species of moderate size with plicate lateral slopes and long to short dorsal adminicula.

(*b*) A group of larger species with non-plicate or very weakly plicate lateral slopes and long dorsal adminicula. This is typified by the form illustrated as *Martiniopsis sp.* 'a' from Ingelara (Campbell 1953).

(*c*) A group of species of the *I. oviformis* (M'Coy) type, with strongly inflated and elongate shells, deeply plicate lateral slopes, and weak to strong dorsal adminicula.

The division between stocks (*a*) and (*b*) may not be definite, but study of larger collections will be necessary before the issue can be clarified. It may be that some of the species included in stock (*a*) have evolved independently from stock (*b*).

Distribution. The genus occurs throughout eastern Australia in rocks which are thought to range in age from Sakmarian to Kazanian. It frequently occurs in profusion, and is one of the most widespread genera in our Permian deposits.

Waagen (1891) described a single specimen referred to *Martiniopsis darwini* (Morris) from the Speckled Sandstone of the Salt Range, India. The specimen is a small brachial valve. None of the internal characters are described, and hence it is impossible to assign the form definitely to *Ingelarella*, but Waagen's statement that 'under the lens one can observe at places a trace of the granulation of the shell, characteristic of the genus, but so far deteriorated by weathering that the grooves in which the granules had been placed have become elongate instead of being round', suggests that it may well belong to that genus.

The fragmentary specimen from the Zewan Beds of Kashmir referred by Diener (1899) to *Martiniopsis* sp. ind. aff. *subradiata* (Sowerby) is badly distorted, and from the description it appears that Diener was not certain even whether it was a pedicle or a brachial valve. It is said to have a very faint radial ornamentation and a punctate and fibrous shell structure. The interpretation of this specimen from the data available is a virtual impossibility.

Reed (1932) has referred two incomplete brachial valves from the Agglomeratic Slate of Kashmir to *Spirifer* (*Brachythyris*) *darwini* Morris. The figures and description

certainly suggest the brachial valve of an *Ingelarella*, except that Reed claims that the shell is minutely punctate, but without the details of the pedicle valve one cannot be certain of this determination.

The Argentinian specimens referred by Harrington (1955) to *Notospirifer darwini* (Morris) closely resemble *I. angulata* sp. nov. The Bonete Formation, from which these fossils come, is considered to be Sakmarian or Artinskian in age. Further discussion of these specimens is included under *Notospirifer*.

Fletcher (1952) has assigned some poorly preserved specimens from the Productus Creek area of New Zealand to *Spirifer* cf. *glaber* Dana (*non* Martin) from N.S.W., this species being an *Ingelarella*. Trechmann (1917) had previously placed specimens from the Maitai Series in the Tasmanian species *Ingelarella subradiata* (G. B. Sowerby).

Three Russian species have been compared with Australian Ingelarellinids—*Spirifer sokolovi* Tscher., *S. supracarbonicus* Tscher., and *Brachythyris kumpani* Yan. (see Tschernyschew 1902, pp. 552–4; Yanischevsky 1935, p. 68). All of these forms are very similar externally to various species of *Ingelarella*. However, in the case of both *S. sokolovi* and *S. supracarbonicus* the external ornament appears to consist of growth lines only, and the internal structure remains virtually unknown. Had the Ingelarellinid ornament been present Tschernyschew would no doubt have observed it, since he did so on *Martiniopsis*. The presence of weak folds in the sinus relates these species to *S. ufensis* and *S. uralicus* (both of which have dental lamellae and ventral adminicula), as was suggested by Tschernyschew himself, and excludes them from *Ingelarella*. Probably *B. kumpani* also belongs to the same species group.

Distribution. In Queensland *Ingelarella* ranges from the lowest to the highest known marine Permian beds, i.e. from the Dilly Formation of the Springsure area to the '*Martiniopsis*' bed above the *Streptorhynchus* zone at the northern end of the Bowen Syncline. It has a comparable range in New South Wales. Current correlations suggest that the time interval involved is from about the Sakmarian to the Kazanian.

In both Pakistan and Argentina the genus appears to be restricted to the lower part of the Permian, but in Argentina this range will probably have to be extended upwards when the faunas of the Permian are better known.

Genus NOTOSPIRIFER Harrington

Type species by original designation: *Spirifer darwini* Morris, from Glendon, Hunter Valley, N.S.W.

Diagnosis. Shell small to medium size; much broader than long; hinge line three-quarters to five-sixths of the maximum width; cardinal extremities rounded; sinus and fold present; fold rounded, flattened, or bearing a shallow median groove; lateral slopes deeply plicate, with three to six plicae; surface with deep, closely packed, sub-circular or slightly elongate pits; thick dental lamellae supported on short, widely divergent adminicula; thick crural plates, but supporting adminicula very weak or absent.

Remarks. Harrington (1955) in describing his new genus figured the syntype BB. 6243 B.M. of *Spirifer darwini* Morris, but he did not formally nominate a lectotype for the species. Therefore I here designate BB. 6243 B.M., from Glendon, N.S.W., figured

Harrington (1955, pl. 23, figs. 7, 11, 12, 14), and figured herein (Pl. 56, figs. 1*a–c*), as the lectotype of *S. darwini* Morris.

Two trips have been made in an attempt to rediscover the locality at Glendon from which Strzelecki collected the types of *S. darwini*, but without success. The type specimens are in a ferruginous sandy matrix. On the bank of the Hunter River in front of Glendon Homestead is an outcrop of the Muree Formation from which I have collected several specimens of *Ingelarella* in a very ferruginous sandy matrix, but no specimens comparable with either of the syntypes has been found. Thus I have had to interpret the species on the basis of the Strzelecki specimens, which I have seen at the British Museum. Harrington has already described these using plaster casts of the originals and notes provided by Dr. Muir-Wood.

As recorded by Harrington (p. 116), Muir-Wood believes the specimens show 'obscure traces of spines which must have covered the whole surface'. In my opinion the surface ornament is not shown on either specimen, and the structures described as spine traces are the result of irregular decortication of the shells. In this connexion two further points are of significance. The typically Ingelarellinid ornament figured by Harrington (1955, pl. 23, fig. 15) is described in the text as 'lamellose-fimbriate' (p. 117), and although Muir-Wood believes that obscure traces of spines are present, no details of the spines themselves have been observed (Harrington, p. 116).

In my opinion the two syntypes are not congeneric. Specimen BB. 6244 has the pedicle umbo broken off, but it is apparent from the general contour of the posterior portion of the valve that the umbo was quite high. The plicae of the lateral slopes are low. The interior of the pedicle valve is not well exposed, but it is almost certain that the muscle field is narrow and bounded by long adminicula lying within the folds bordering the sinus. The brachial valve has relatively long widely divergent dorsal adminicula. The specimen almost certainly belongs to *Ingelarella*. Dr. Cooper, U.S. National Museum, has kindly sent plaster casts of specimens assigned to *S. darwini* in the collection from Glendon described by Dana (1849). This specimen (Pl. 56, figs. 3*a*, *b*) compares favourably with BB. 6244 in all features including the dorsal adminicula, which diverge outside the first plica lateral to the fold in a way unobserved in any other species. I am convinced that the two specimens are conspecific. The ventral adminicula are well exposed and confirm the tentative observation made on these structures in BB. 6244. Unfortunately no surface ornament is preserved.

The lectotype BB. 6243, on the other hand, has a very low pedicle umbo, and a very transverse outline. The folds on the lateral slopes are rather strong. The ventral adminicula are short and widely divergent, lying outside the folds bordering the median sinus. The dorsal adminicula, if present, must be very short. All of the species (four in number) with this combination of characters which have come under my notice also have a surface ornament of rather deep pits. In the absence of direct evidence in support of this from the actual lectotype, and in view of my failure to discover topotypes, the surface characters of these species have been attributed to *N. darwini* (Morris).

Distribution. No species yet described from outside eastern Australia is considered to belong to this genus. As is indicated in the discussion on *Ingelarella*, the Indian forms referred to *Martiniopsis darwini* (Morris) by Waagen (1891) and *Spirifer* (*Brachythyris*) *darwini* Morris by Reed (1932), and the Argentinian specimens referred to the same

species by Harrington (1955), are considered to belong to *Ingelarella* rather than to *Notospirifer*. In Queensland the genus ranges from the Homevale Beds to the *Streptorhynchus* zone, i.e. Sakmarian–? Kazanian. Its range in the other eastern States is unknown.

SIMILAR GENERA

The spiriferid stock has at several times developed smooth or pauci-plicate homeomorphic groups (see Buckman 1908), many of which have, at some time or another, been referred to *Martiniopsis*.

Warrenella Crickmay, from the Middle and Upper Devonian of North America, has the conformation, smooth fold and sinus and lateral slopes, thickened umbo and dental lamellae of an *Ingelarella*, and there are also resemblances in the fine surface ornament which in *Warrenella* consists of 'short (0·1 mm.) radial threads disposed in concentric groups 1·5 mm. apart' (Crickmay 1953, p. 598). Yet the peculiar mode of thickening in the pedicle umbo, the presence of a deltidium, the unusually thickened brachial valve, and the ridged rather than pitted micro-ornament arranged on a linear rather than a quincuncial pattern, show beyond reasonable doubt that this genus is genetically quite unrelated to the Ingelarellinids.

The relationship of *Martinia* to *Martiniopsis* has been discussed by several authors since Waagen (1883), and notably by Etheridge (1892, p. 237). There is no doubt that the two genera can be distinguished by the presence or absence of ventral adminicula, and by the absence of a pitted surface layer in *Martinia*, but there may also be differences in the intimate structure of the shell substance. For example, the species from the Permian of Mongolia assigned to *Martinia* by Grabau (1931) all have a smooth surface except for fine irregular concentric growth lamellae, but the exfoliated surface has numerous radiating striae which give rise to delicate pustules where they cross the growth lines. This has never been observed in any Australian Ingelarellinids.

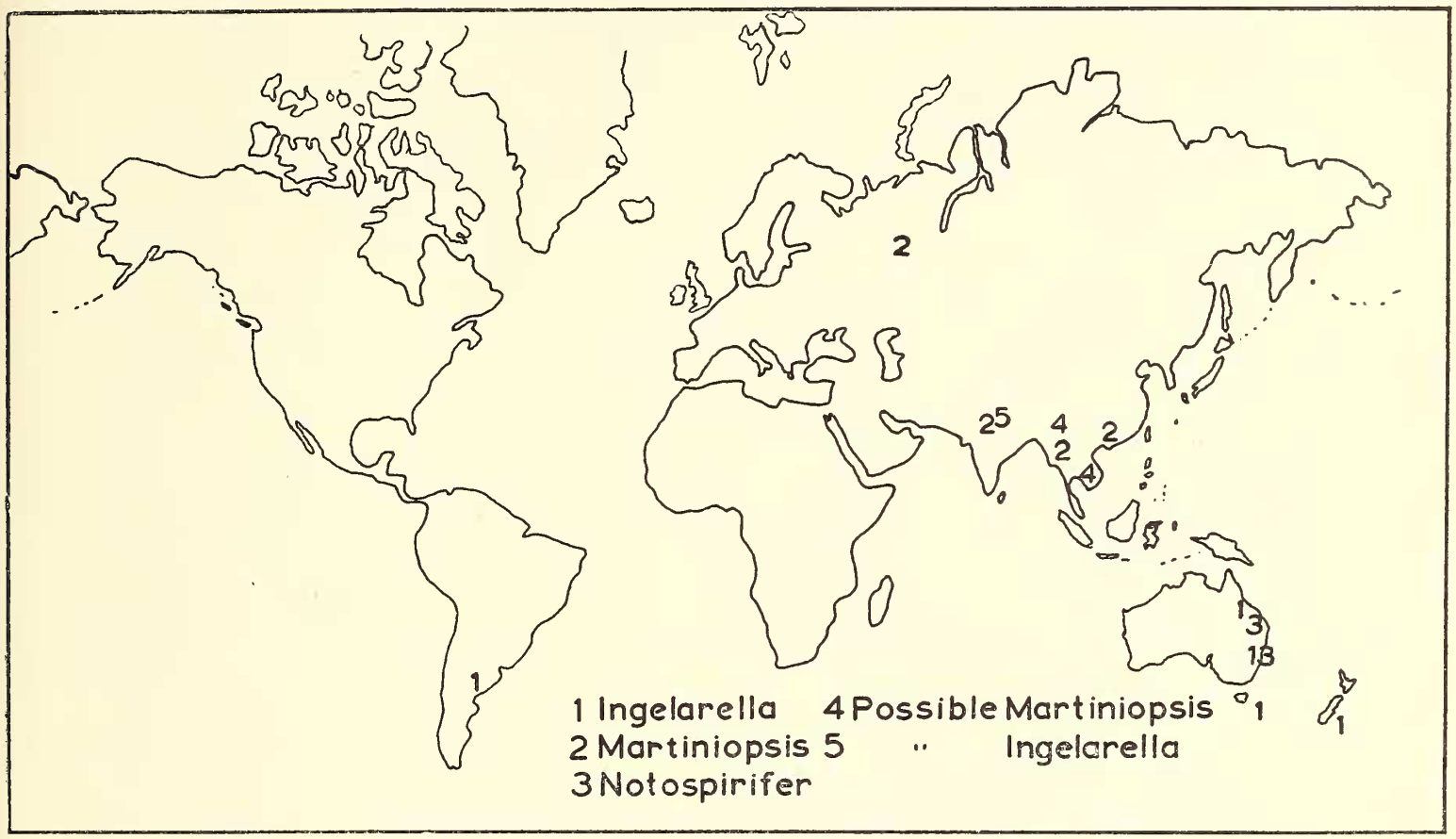
From the lower Carboniferous of China comes a large group of species referred to the genus *Martiniella* Grabau, which in external form and the presence of ventral adminicula resembles *Martiniopsis*. On the evidence available at present they may be distinguished from this latter genus by the absence of dorsal adminicula, and by the presence of a finely striate micro-ornament (Chu 1933, p. 51).

Of greater interest is the genus *Eomartiniopsis* Sokolskaya, from the Tournaisian of the Moscow Basin. Both in general form and the development of plates in each valve, this genus resembles the *Martiniopsis*. It is difficult to assess the relationships of the surface ornament which is said to be finely pitted. The semi-quincuncial arrangement, however, does not resemble that of either *Ingelarella* or *Notospirifer*. The possibility must still be entertained, however, that this genus belongs to the Ingelarellinae.

To accommodate species of the type previously referred to *Martiniopsis baschkirica* Tschernyschew and *M. aschensis* Tschernyschew, Fredericks (1919) erected the genus *Elivella*. Both of these species are characterized by a very narrow fold and sinus, multiplicate lateral slopes and a very finely striate surface ornament. In the case of *M. baschkirica*, Tschernyschew records that the folds bordering the sinus bifurcate at about the mid-length of the valve and that the test exhibits a fine 'punctstructur'. These features are sufficient to exclude *Elivella* from the Ingelarellinae.

Mentzelia Quenstedt has as type species *Spirifer medianus* Quenstedt from the Muschelkalk of Silesia, but Douglas has described a Permian species, *M. persica*, from

Iran (Douglas 1940). In external form and the presence of dental lamellae this species is not unlike *Martiniopsis*, but internally it is distinguished by the presence of a high median septum in the pedicle valve, and a thick hinge plate of a kind unknown in the Ingelarellinae, in the brachial valve. In addition, the surface is described as 'smooth with occasional concentric growth-lines' (Douglas 1940, p. 332), and the shell structure is said to be fibrous and impunctate. Certain Triassic species ascribed to *Mentzelia* are, however, claimed to be punctate (Trechmann 1917, p. 228).



TEXT-FIG. 4. Distribution of the genera of the Ingelarellinae.

Ingelarella angulata sp. nov.

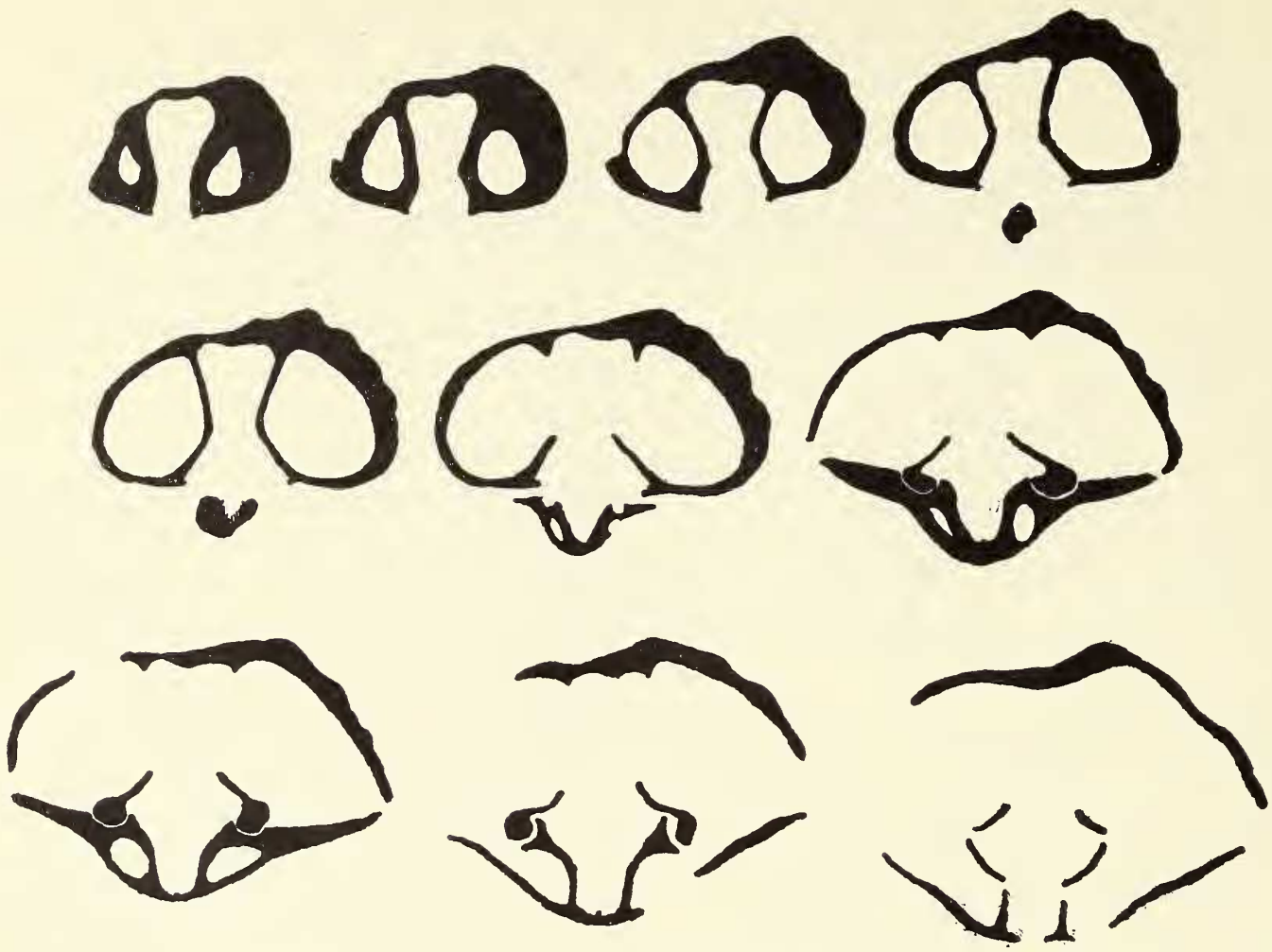
Plate 56, figs. 4*a–c*; Plate 57, figs. 1–5

1953 '*Martiniopsis*' sp. b, Campbell, p. 10, pl. 4, figs. 4–9; pl. 5, figs. 4–6.

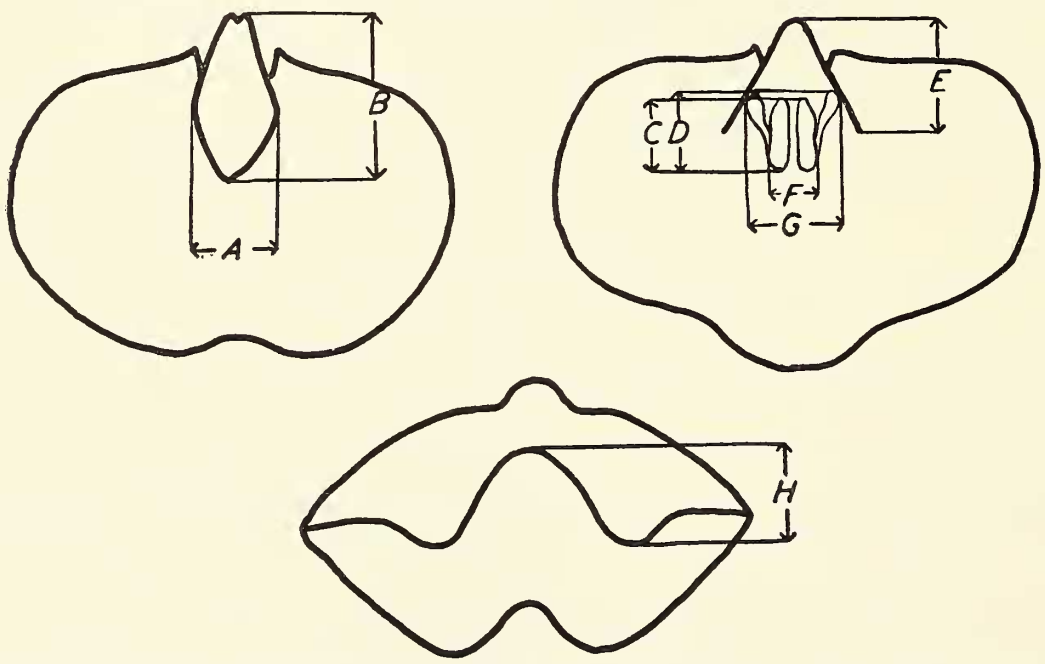
Holotype. F. 14295, U.Q.; from Ingelara Shale, Dry Creek, ½ mile upstream from the road crossing, Ingelara Station, south-west of Springsure, Queensland: *paratypes*, F. 14294 and F. 14296–7; F. 15695–F. 15697 and F. 24834 and F. 24837, U.Q.

Diagnosis. Medium-sized, plicate shells usually with an open V-shaped median sinus; fold bearing a median furrow; ventral adminicula long, thin and curved inwards anteriorly; dorsal adminicula slender, upright, and extending one-quarter to one-third the length of the valve.

Description. The shells are of medium size for the genus, with a moderately convex pedicle valve and a somewhat less convex brachial valve. The hinge line is approximately five-eighths of the maximum width of the shell.



TEXT-FIG. 5. Serial sections of a topotype of *I. angulata* sp. nov. taken at 1 mm. intervals. ×1.



TEXT-FIG. 6. Diagrams illustrating the method of taking the measurements listed in the table of dimensions. A = width ventral muscle field; B = length ventral muscle field; C = length central dorsal adductors; D = total length dorsal adductors; E = length dorsal adminicula; F = width central dorsal adductors; G = total width dorsal adductors; H = height fold. Diagrams are of an internal mould.

The ventral valve is most convex towards the incurved umbo. The dental ridges are thin but wide. The median sinus is clearly defined, the transverse sections being open V-shaped in most specimens, though in others there is a tendency towards a flatter bottom. A shallow median groove is invariably present. The sinal angle averages 24° (range 18–30° over seven specimens). The gently convex lateral slopes each carry four low, rounded plicae which rapidly diminish in size laterally, the most lateral one frequently being indistinct.

The brachial valve is almost oval in outline and its length is approximately three-quarters of the width. It is usually evenly convex longitudinally, but it may be slightly more convex toward the umbo. The lateral slopes are gently convex. The median fold is of moderate height, not breaking the general contour of the valve, and its central portion is occupied by a shallow furrow.

Because of the nature of the preservation the surface pits are rarely seen.

Interior. The pedicle valve has only slightly thickened umbonal shoulders. The ventral adminicula extend approximately one-third the length of the valve and tend to curve together toward their anterior tips. Transverse sections show the planes of the adminicula converging toward each other at angles between 10° and 35°. In these sections the convergence of the dental lamellae varies according to the position of the section, the angle at a position just posterior to the teeth being in the vicinity of 80°–90°. The dental lamellae are relatively unthickened and on their outer surfaces the extension of adminicular tissue is never thick. The teeth are large bulbous structures which are hooked inwards. Preservation in a hard calcareous sandstone which does not permit the exposure of internal detail by cleaning or etching, makes the muscle field difficult to observe, but it is known to be long and narrow.

Dimensions (in mm.)

Length	*Width*	*Height*	*Length brachial valve*	*Height fold*	*Length ventral muscle field*	*Width ventral muscle field*	*Length central dorsal adductors*	*Width central dorsal adductors*	*Total length dorsal adductors*	*Total width dorsal adductors*	*Sinal angle*	*Length dorsal adminicula*
					Mt. Coma, near Mt. Britton							
51	65	33	43	8	..	11	..	..	..	..	..	17
50	53	32	42	12	*c.* 26	13·5	..	3·5	..	9·5	..	19
48	54	..	38	9	*c.* 23	8·5	..	..	..	..	..	18
46	57	28	40	6·5	20	9	12	2·5	17	8	23°	17
40	*c.* 52	26	35	7	18	8	9	2·5	12	6	..	18
..	47	25	..	..	..	9	9	2	10	5·5	..	12
33	40	19	29	4	14	8	..	2	..	5	24°	12
					Dry Creek, Ingelara							
..	*c.* 65	..	..	..	*c.* 25	*c.* 8	..	..	..	..	..	24
49	60	34	45	10	*c.* 20	7	..	..	..	..	18°	13
40	51	32	35	9	..	..	..	..	..	..	23°	..
35	40	21	31	5	..	..	..	..	..	..	23°	11
30	34	21	28	7	..	..	..	..	..	..	26°	..

The dorsal adminicula are long and tapering, extending from one-quarter to one-third the length of the valve. They diverge at angles of from 10° to 15° along the floor of the valve. In transverse section they are slightly divergent in the umbo, but they rapidly become almost vertical except for their ventral edges which are slightly flexed outwards. Anterior to their point of origin the descending lamellae are set at about 45° to each other, but as they descend they gradually tend to become parallel. The spires are formed

of approximately twenty volutions each. The central adductor scars are apparently rather narrow, but the details are not visible. They are separated by a fine, sharp keel. The cardinal process consists of numerous fine platelets within the notothyrial cavity. There is no sign of a boss or projection for the support of this structure. Towards the front of both valves there are numerous, closely set radial markings which are apparently pallial in origin. They are better preserved on the Mt. Coma specimen described below (see Pl. 57, figs. 3, 5).

Remarks. The population from the type locality is very variable particularly with respect to height of the shell, the degree of development of the plicae, and the shape of the sinus.

There is a resemblance to one of the syntypes (BB. 6244) of *Spirifer darwini* Morris, but this latter form is distinguished by its shorter, more divergent dorsal adminicula, its narrower median fold, and shallower, flatter bottomed sinus.

Specimens from other localities. Specimens probably referable to this species have been obtained from Mt. Cona (Mt. Coma) northwest of Homevale Station, via Nebo, on the

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EXPLANATION OF PLATE 56

Figs. 1–4 are natural size; Figs. 5–12 are ×5.

Figs. 1*a–c*. *Notospirifer darwini* (Morris). Ventral, dorsal, and anterior views of a plaster cast of the lectotype. Note the very short and widely divergent ventral adminicula; BB. 6243 B.M., from Glendon, Hunter Valley, N.S.W.

Figs. 2–3. *Ingelarella sp.* 2*a–c*, Ventral, dorsal, and anterior views of the second of Morris's syntypes of *Spirifer darwini*, BB. 6244 B.M., from Glendon, Hunter Valley, N.S.W. 3*a–b*, Ventral and posterior views of a plaster cast of a specimen collected by the Wilkes Expedition from Glendon, and referred by Dana to *Spirifer darwini*, 3634 U.S. National Museum.

Figs. 4*a–c*. *Ingelarella angulata* sp. nov. Ventral, dorsal, and anterior views of a small paratype from the type locality, F. 14297 U.Q.

Figs. 5–7. *Notospirifer spp.* Three undescribed species. 5, Small patch of surface shell showing the almost equidimensional surface pits filled with white matrix; F. 21945 U.Q. 6, External mould of part of the shell surface showing the infillings of the deep, densely packed pits. These infillings appear to be more or less lozenge shaped over most of the surface due to the fact that they are directed at an angle to the shell and hence have not been photographed end-on. In the bottom left-hand corner they are almost end-on; F. 3055 U.N.E. 7, External mould of part of shell surface. Similar remarks to those above apply; F. 15826 U.Q.

Figs. 8–12. *Ingelarella spp.* Five undescribed species. 8–9 and 11–12 are external moulds, while 10 is the actual shell surface. Note the variation in size, shape, and density of the pits. 8, F. 3228 U.N.E. 9, F. 3111A U.N.E. 10, F. 15686 U.Q. 11, F. 2992B U.N.E. 12, F. 3318 U.N.E.

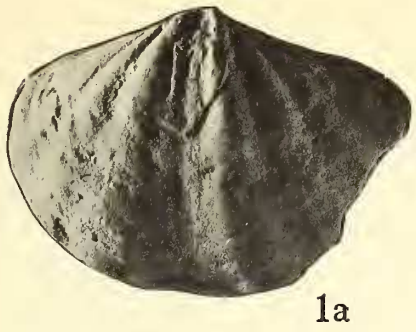
Fig. 13. *Notospirifer sp.* Thin section across the anterior part of the shell of the species shown in fig. 7 above. What appears to be a fringe of bristle-like spines is the result of oblique sectioning of the surface pits. ×3·2.

Fig. 14. *Ingelarella sp.* Thin section of the lamellar layer of a shell showing some of the spicular structures mentioned on p. 335. ×40.

EXPLANATION OF PLATE 57

All specimens natural size.

Figs. 1–5. *Ingelarella angulata* sp. nov. 1*a–c*, Ventral, dorsal, and anterior views of the holotype, F. 14295 U.Q. 2*a–b*, Dorsal and ventral views of an internal mould of a paratype from the type locality, F. 24834 U.Q. 3, Dorsal view of an internal mould of a paratype from the type locality, F. 24837 U.Q. 4*a–c*, Ventral, dorsal, and anterior views of a paratype from the type locality with the shell partly removed, F. 15696 U.Q. 5*a–c*, Dorsal, ventral, and anterior views of an internal mould of a paratype from Mt. Coma, F. 2126 G.S.Q.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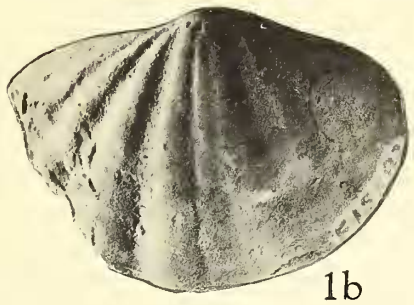
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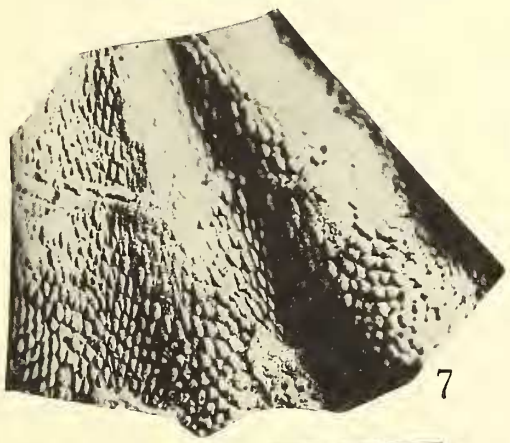
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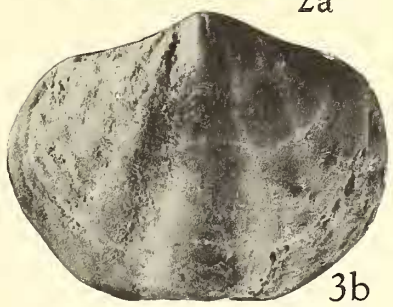
2a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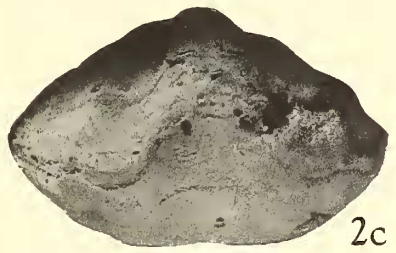
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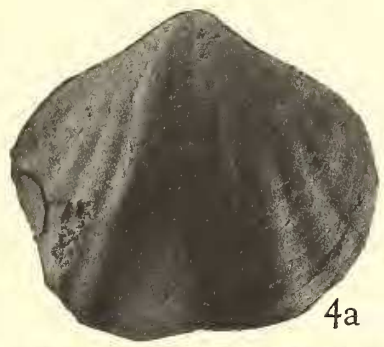
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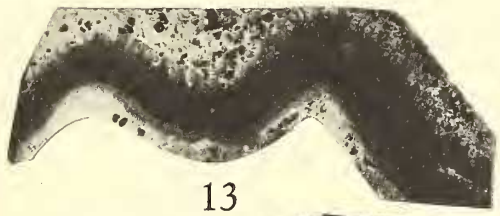
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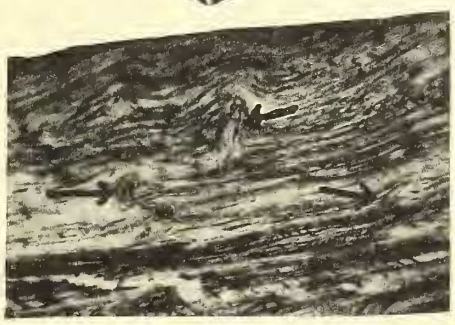
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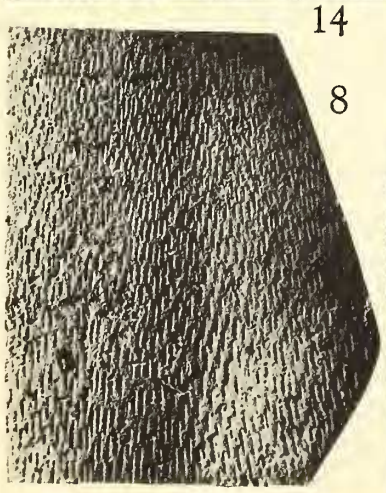
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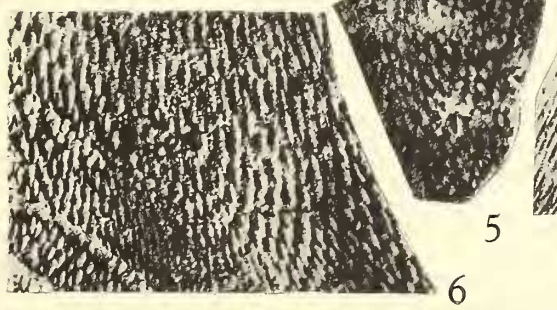
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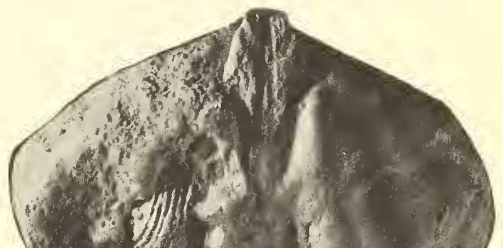
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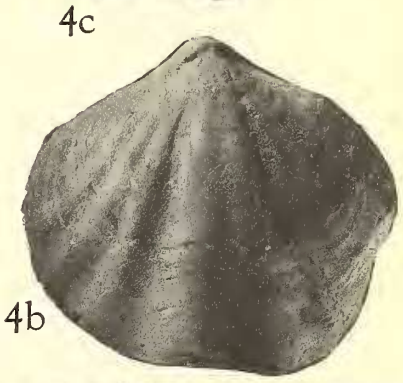
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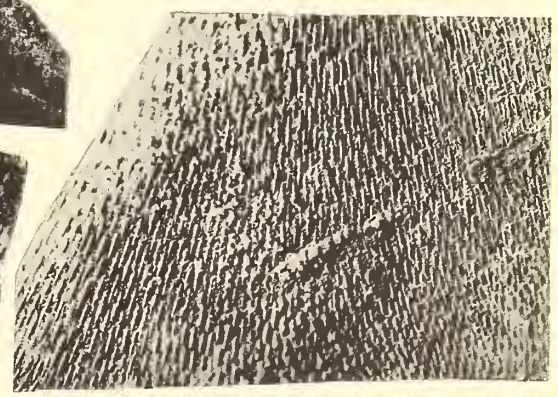
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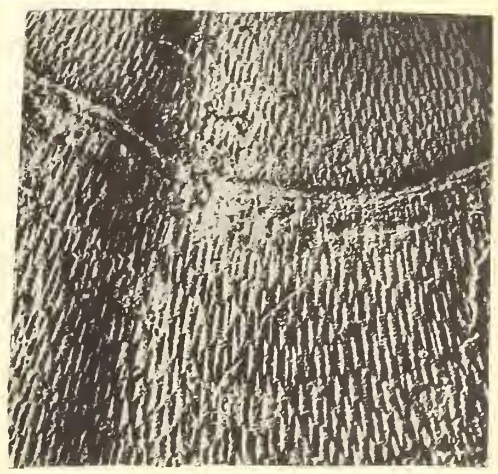
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CAMPBELL, Ingelarellinae